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ARTICLE

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Small-scale spatial distributions of long-finned pilot whales change over time, but foraging hot spots are consistent: Significance for marine wildlife tourism management

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Abstract

Data collected opportunistically aboard marine wildlife tourism vessels are an inexpensive source of spatial information on the target species. Although these data are often challenging to analyze, they can be used to monitor spatiotemporal changes in species distribution and behavior. Disruptions from whale-watching vessels to behaviors such as foraging can be particularly harmful to cetaceans, but impacts could be reduced if areas essential for these sensitive behaviors are identified. We used data collected onboard whale-watching vessels to explore space-use patterns in long-finned pilot whales (*Globicephala melas*) off northern Cape Breton Island, Canada, an area where tourism is essential. Encounters with pilot whales between 2011–2016 occurred twice as far offshore than during 2003–2006 and 2008, and foraging activity decreased. Despite the changes in distribution and activity budgets, we identified two hot spots of foraging activity that persisted through time. These identified foraging hot spots comprised only a small proportion (20 km^2) of the range used by whale-watching vessels. Adaptive local management (e.g., voluntary codes of conduct) focused on limiting interactions in these energetically important areas may help reduce any potential impacts from whale-watching and promote the continued viability of the whale population and the tourism industry that relies on it.

KEYWORDS
activity budget, bivariate Moran's I, Getis-Ord G_i*, *Globicephala melas*, long-finned pilot whale, whale-watching

1 | INTRODUCTION

Opportunistic data collected aboard marine wildlife tourism vessels can provide valuable information on the ecology of target species and help monitor shifts in their occurrence. Marine wildlife tourism is increasing, with thousands of operations worldwide (O'Connor et al., 2009). Whale-watching is economically valuable, generating US$2.1 billion globally in 2008 (O'Connor et al., 2009), and it can be used as an inexpensive platform to collect ecological data (e.g., Currie et al., 2018; International Whaling Commission [IWC], 2017). Many whale-watching operators already collect information on species occurrence, distribution, and behavior within local areas (e.g., Hupman et al., 2015; Stockin et al., 2009). The use of whale-watching vessels as platforms of opportunity for research has been widely documented (e.g., Macleod et al., 2004; Weinrich, 1998) and the International Whaling Commission has discussed at length the use of whale watching as platforms of opportunity (e.g., IWC, 2001, 2006). While data collected aboard whale-watching vessels are becoming increasingly common, this type of opportunistic data is often spatially biased and challenging to analyze compared to standardized surveys (Currie et al., 2018; Hupman et al., 2015; IWC, 2017; Noren & Hauser, 2016). However, as we show here, whale-watching data can be used to understand spatiotemporal changes in species distribution and behavior and inform the local management of the marine wildlife tourism industry.

Since whale-watching tourism has the potential to negatively impact cetaceans (Christiansen et al., 2013; Meissner et al., 2015; Stockin et al., 2008), using opportunistic data to monitor target species is particularly important. For an in-depth review of the impacts of whale watching on cetaceans, see New et al. (2015) and Parsons (2012). Cetaceans are susceptible to disturbances from human activities (e.g., Lusseau et al., 2009; Parsons, 2012; Williams et al., 2006). Behaviors most sensitive to disturbance can be species-specific, but commonly include foraging (Christiansen et al., 2013; Meissner et al., 2015; Stockin et al., 2008) and resting (Lusseau & Higham, 2004; Tyne et al., 2015). Disruption to sensitive behaviors can cause targeted species to alter habitat use and shift local distributions to avoid vessels (Bejder et al., 2006; Higham et al., 2016; Lusseau, 2005). In turn, such changes in distribution and behavior can have adverse effects on the whale-watching industry. For example, if cetaceans shift their distribution farther from port to limit their interactions with vessels (e.g., Bejder et al., 2006; Lusseau, 2005; Rako et al., 2013), operators will have to travel farther and spend more resources to get to the whales. This feedback between the behavior of whales and the tourism industry can hinder our ability to use opportunistic data to understand changes in the distribution and space use of cetaceans. However, it is easier to use such data if the cetacean sightings are accompanied by whale-watching vessel location data (e.g., GPS boat tracks) logging all areas searched during a trip. These boat data can be used to create effort layers and define areas that were searched but had no cetacean sightings. Data on search effort can help disentangle the spatial changes in whale-watching vessels from spatiotemporal patterns of cetaceans.

The response of target species to whale-watching vessels and the viability of the whale-watching industry are tightly linked. Thus, limiting interruptions to sensitive behaviors to reduce possible adverse effects on targeted species can be vital for both species protection and the industry's sustainability. Acknowledgment of this within the whale-watching industry has led to the development of "codes of conduct" and other self-regulatory measures to reduce negative impacts on the whales (e.g., Allen et al., 2007; Guerra & Dawson, 2016), which the IWC has supported through the creation of an online whale-watching handbook (IWC, 2020). It can be advantageous to focus mitigation measures in areas where the energy-maintaining behaviors sensitive to disturbance occur (Ashe et al., 2010; Noren & Hauser, 2016; Smith et al., 2013). As behaviors most at risk to disturbance can be primarily confined to particular habitats (e.g., Tyne et al., 2015), identifying sensitive areas which overlap with the range of whale-watching operations can help develop appropriate mitigation measures. Reducing vessel activity in such areas can offer significant protection to whales with little disruption to the tourism industry that depends on them (Lusseau, 2004).

Our goals were to use effort and sightings data to identify trends over the years in the distribution of long-finned pilot whales (*Globicephala melas*) and to use behavioral data to identify areas where whales conduct important behaviors and whether these areas change through time. The long-finned pilot whales found in Pleasant Bay, Nova Scotia, Canada, are a target species for an important tourism industry that operates during the calving season (July–September), a vulnerable period in the life-history of whales. Free-ranging long-finned pilot whales exposed to anthropogenic noise can drastically reduce time spent foraging (Isojunno et al., 2017). Such reductions in foraging have been shown to have substantial energetic costs in related killer whales (*Orcinus orca*; Williams et al., 2006). Thus, we were interested in investigating the temporal persistence of foraging hot spots. Our study is part of a long-term research partnership with a whale-watching operator in Pleasant Bay. The project's overall goal is multifaceted and includes research on the ecology and behavior of long-finned pilot whales (e.g., Augusto et al., 2016, 2017; Zwamborn & Whitehead, 2017). Since the early 2010s, whale-watching operators have observed yearly variability in the occurrence of pilot whale sightings and had to change their practices in response to shifts in the whales' local distributions. To describe changes in whale distribution, we compare the spatial patterns in the long-finned pilot whale observations collected from whale-watching vessels from 2003 to 2016. To identify areas where limiting interactions with whales would contribute the most to the conservation of the pilot whales while minimizing disruptions to whale-watching operators, we (1) identify regions where activity states, such as foraging, are predominantly observed and (2) determine whether foraging hot spot locations are consistent or changing over time.

2 | METHODS

2.1 | Data collection

The research was conducted from 2003 through 2016 in nearshore waters off Pleasant Bay, Nova Scotia, Canada in the Gulf of St Lawrence (46.83°N, 60.80°W). Field seasons occurred in July and August of each year when long-finned pilot whales are found predictably in the area. Researchers collected data aboard a 12.8 m commercial whale-watching vessel, which operated under Fisheries and Oceans Canada whale-watching guidelines (Fisheries and Oceans Canada [DFO], 2012, 2018). The whale-watching vessel made up to five daily trips lasting 2–4 hr, between approximately 0945 and 1900 Atlantic Daylight Time (UTC-3), and only ran during fair weather when sea states were ≤4 on the Beaufort scale.

The whale-watching captains selected the whale groups to observe, with a bias towards those found closest to the harbor. An encounter, the spatiotemporal unit for a group of whales (Ottensmeyer & Whitehead, 2003), began when the vessel was within 200 m of the group. Encounters were terminated once whales were out of sight for longer than 10 min. The vessel approached groups slowly from the side or behind (DFO, 2012, 2018).

Behavioral data were collected through group focal follows and instantaneous scan sampling (Mann, 1999) at 5 min (2003–2006) or 10 min (2008, 2011–2016) intervals. To standardize data across years, we kept only observations made in 10 min increments after the start of the encounter, even when data were collected every 5 min. Behavioral data included the group activity states of foraging, resting, socializing, and traveling, with our definitions resembling those used by others to classify cetacean behavior (Heimlich-Boran, 1988; Meissner et al., 2015; Noren & Hauser 2016; Table 1). As long-finned pilot whales generally synchronize their behavior with other group members, the activity state performed by the majority of the group was recorded. Any bias in the activity state of pilot whales from the presence of a whale-watching vessel is assumed to be consistent throughout the years. During encounters, the pilot whales' location was recorded every 5 min using a hand-held Global Positioning System (GPS) unit. For a subset of the years (2003–2006, 2011–2016), the vessels' locations throughout the trip were also recorded every 5 min.

2.2 | Determining the predominant activity of encounters

Pilot whales often perform the same activity for long durations; thus, our behavioral scan data generally included repeated and dependent records of the same state. To reduce autocorrelation, we used the predominant state of an encounter, i.e., the most frequently recorded activity state in an encounter. When multiple activity states were recorded during a single scan, each was allocated an equal portion of that scan when calculating the predominant state. If there was a tie for the predominant behavior across multiple states, all of these states were included in the analysis but proportionally down-weighted (e.g., 0.5 Foraging, 0.5 Resting). All data manipulation and statistics were performed in R unless otherwise stated (R Core Team, 2013).

2.3 | Spatial analysis of encounter locations

We performed spatial analyses to assess potential changes in encounter distribution using ArcMap 10.6 (Environmental Systems Research Institute, 2011) and GeoDa 1.12.01 (Anselin, 2018). Encounter locations were based on the start time and position of each encounter. We chose an intermediate resolution grid system (2 × 2 km) to decrease the potential spatial autocorrelation between cells while retaining enough cells for analyses (Atkinson & Tate, 2000; Potter et al., 2016).

We estimated the rate of pilot whale encounters in each year while accounting for the search effort. Each day, we assessed whether each grid cell was searched and whether it resulted in at least one encounter. Doing so accounted for the nonindependence of observations associated with whale-watching vessels frequently returning to locations where whales were seen earlier. Cells were assessed each day as being “searched” or “not searched” dependent on whether a vessel track passed through them. To determine the encounter rate, we divided the number of days with encounters, by the number of days searched within each cell. Data from 2008 were unavailable for this analysis due to a high degree of incomplete vessel track data, which could potentially bias search effort estimates (Table S1).

To investigate potential explanations for the changes in distribution, we assessed whether pilot whales were moving farther from Pleasant Bay harbor specifically, or whether movement offshore was unrelated to the harbor's

TABLE 1 Definitions of the four activity states for long-finned pilot whales (Senigaglia & Whitehead, 2012; Zwamborn & Whitehead, 2017).

Activity state	Definition
Forage	Minimal surface behavior with prolonged fluke dives, echolocation, buzzing, no directional movement, birds often foraging nearby.
Rest	Travel slower than boat idle speed (~5 km/hr), short dives, logging behavior at the surface.
Social	Interaction with conspecifics, active surface behavior, body contact between individuals, can include sexual behaviors, no directional movement, short dives.
Travel	Steady directional movement faster than idle boat speed (~5 km/hr), variable diving patterns.

position. This analysis is based on the assumption that a localized shift in pilot whale distribution away from the harbor would indicate that the increased whale-watching vessel traffic originating from the harbor is a driving factor. For each target (harbor or nearest point on the shore), we estimated a mean encounter distance each year. Rather than merely averaging the distance between the encounters and target for all encounters, we calculated a weighted average to account for spatiotemporal autocorrelation and search effort. We took the mean of the distances between the center of each grid cell and the target, weighted by the cell's normalized encounter rate.

2.4 | Temporal variation in encounter rate and location

To assess the evidence for the decreased sightings in recent years reported by whale-watching operators, we compared yearly encounter rates and the location of encounters. We performed two methods of changepoint analysis; first using the R package “changepoint” employing the Pruned Exact Linear Time (PELT) method with a Changepoints for a Range of Penalties algorithm (CROPS) penalty (Haynes, 2017; Killick, 2012), and second using the R package “bcp” for Bayesian analysis (Erdman & Emerson, 2007). These analyses showed a clear divide in the locations of encounters, where encounters between 2003–2006 and 2008 were closer to the harbor and shore than during 2011–2016.

We then evaluated whether this change in distribution was correlated with the encounter rate and pilot whale activity by comparing these two periods. We compared the encounter rate from the first period (2003–2006 and 2008) to the second period (2011–2016) using a likelihood ratio *G*-test, with the null hypothesis that overall encounter rates between periods were the same. To assess whether the increase in encounter distance correlated with a change in pilot whale activity, we compared the activity budgets of pilot whales between the two periods. To accomplish this, we used a likelihood ratio *G*-test for contingency tables, with the null hypothesis that the probability of a group of pilot whales being observed in any behavioral state was the same in both periods.

2.5 | Hot spots of activity states

We wished to identify areas where specific activity states were concentrated, which we referred to as activity-specific hot spots, and determine whether these hot spots altered with the observed changes in the overall distribution. For each activity state, we calculated the proportion of encounters in each cell for which it was assigned as the predominant activity state. We retained cells containing ≥3 encounters to eliminate cells where whales were rarely seen while maintaining the connectivity of the spatial grid. To identify hot spots, we used Getis-Ord G_i^* to assess whether the activity state occurs in a cell and its neighbors at a higher-than-average rate compared to its overall occurrence across all cells (Getis & Ord, 1992; Ord & Getis, 1995). We used the queen configuration for spatial weights: where all adjacent cells sharing edges and corners of the local cell are considered spatial neighbors. Island cells (i.e., cells with no neighbors) were removed. We used permutation inference in GeoDa (99,999 permutations) to assess whether the occurrence of each activity state was spatially random across all cells (Anselin, 2018; Anselin et al., 2006). While a pseudo *p*-value was calculated for each cell, only neighboring values were permuted, potentially making conventional methods of Bonferroni correction and false discovery rate too conservative (Brunsdon & Charlton, 2011; de Castro & Singer, 2006; Gelman et al., 2012). To account for potential problems associated with multiple comparisons, we interpret hot spots as clusters of higher occurrence values instead of labeling them as statistically significant clusters, as suggested by Efron and Hastie (2016). We display the range of pseudo *p*-values for more informative descriptions of the degree of clustering.

We used bivariate Moran's I to evaluate the consistency of activity hot spots between periods (Anselin, 2018; Anselin et al., 2006). The bivariate spatial correlation was determined using a local cell from the first period paired with neighbors from the second period. We only included cells overlapping in both periods with adequate numbers of encounters. We used the queen configuration for spatial weights and fixed the local cell's value in the first period and permuted values of neighboring cells from the second period (99,999 permutations). A consistent hot spot required a high proportion of an activity state in the local cell of the first period and the neighboring cells of the second period (Anselin, 2018; Anselin et al., 2006).

To assess the impacts of restricting access of whale-watching vessels to essential areas, we estimated the overall encounter rate when consistent foraging hot spot encounters were removed. To do this, we calculate the overall encounter rate per trip as above but for all years. We then recalculated the overall encounter rate removing all encounters within cells where the Moran's I analysis for consistency of hot spots returned a p-value < .05.

3 | RESULTS

3.1 | Yearly encounter rate and spatial distribution

Data used in the analysis were collected over 531 days and 1,774 trips. There were 2,361 encounters with long-finned pilot whales, 2,162 (91.6%) of which were spatially referenced and used in the analysis. The maximum (2.0) and minimum (0.7) yearly encounter rates per trip occurred in 2008 and 2015, respectively (Figure 1, Table S2). The spatial distribution of encounter locations and search effort both expanded with time (Figure 2). A change in encounter distribution was identified by the changepoint analysis and detected a period (2003–2006, 2008) when whales are close to shore and the harbor and a second period (2011–2016) when whales are farther away (Figures 3 and S1). Encounters occurred an average of 3.27 km farther from Pleasant Bay harbor and 2.71 km further offshore in the second period (Figure 3). In contrasting the two periods of encounter spatial distribution, encounter rate was significantly lower in the second period ($G = 70.98$, $df = 1$, $p < .001$), dropping from 1.57 ± 0.28 (mean ± SD) encounters per trip in the first period to 1.09 ± 0.24 in the second period.

3.2 | Hot spots of activity

The activity of pilot whales shifted with the change in distribution. Local activity budget varied significantly between the first and second periods ($G = 23.7$, $df = 3$, $p < .001$). The proportion of foraging decreased from 30.7% ± 13.4%

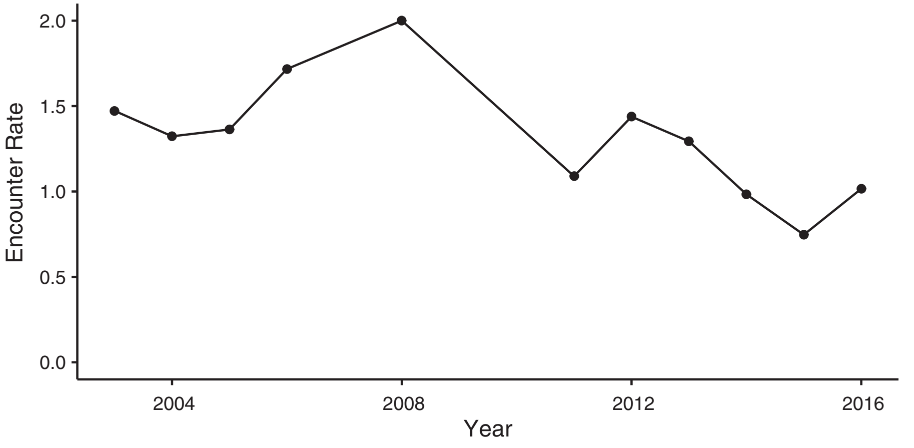


FIGURE 1 The rate of encountering long-finned pilot whales near Pleasant Bay, NS from 2003–2006, 2008, and 2011–2016.

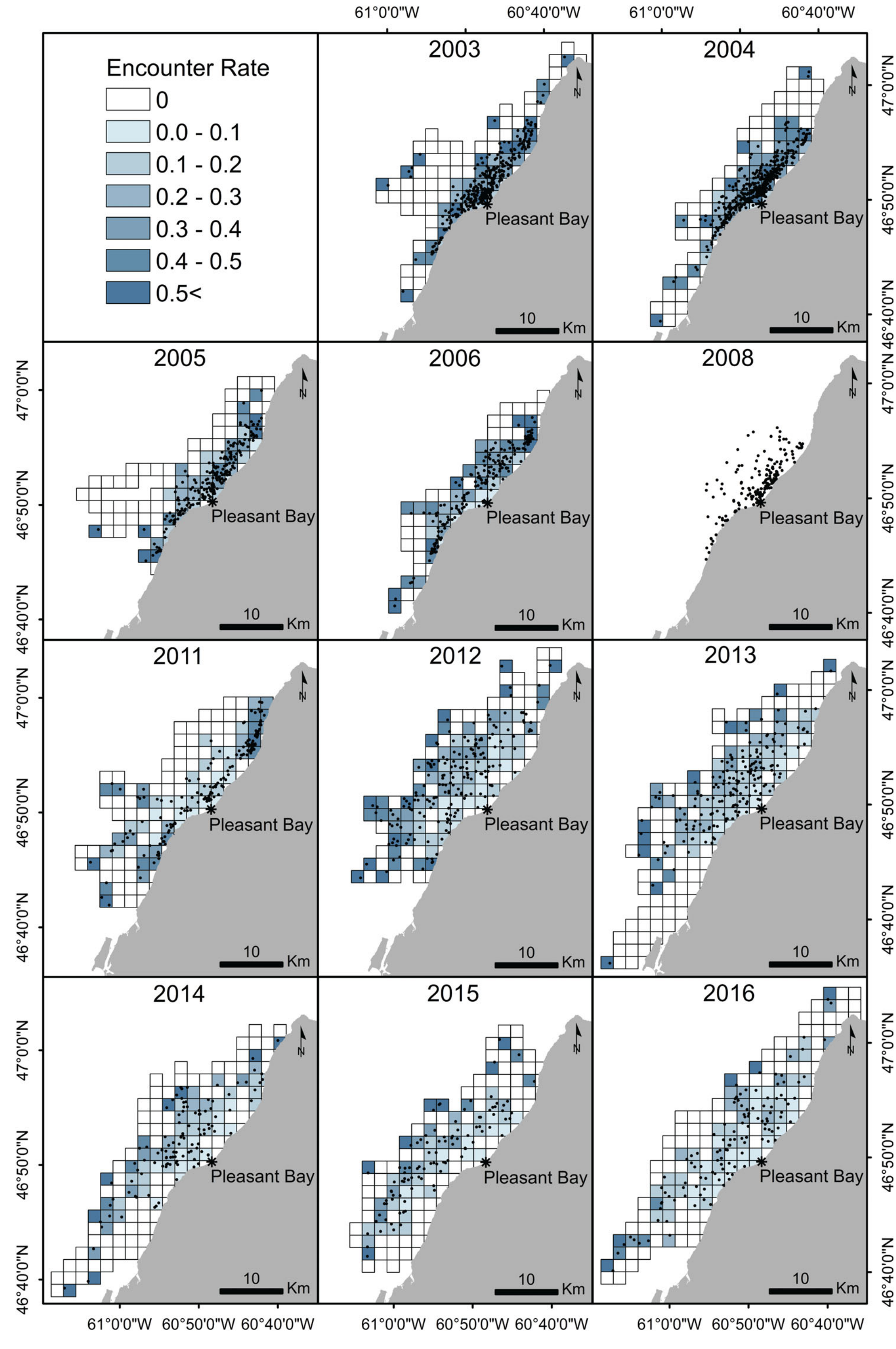


FIGURE 2 The encounter locations (black dots) and encounter rates (cell shading) of long-finned pilot whales around Pleasant Bay, Nova Scotia. Cells are 4 km^2. Note that while we present the encounter locations of 2008, the cell encounter rates are unavailable due to incomplete vessel tracks (Table S1).

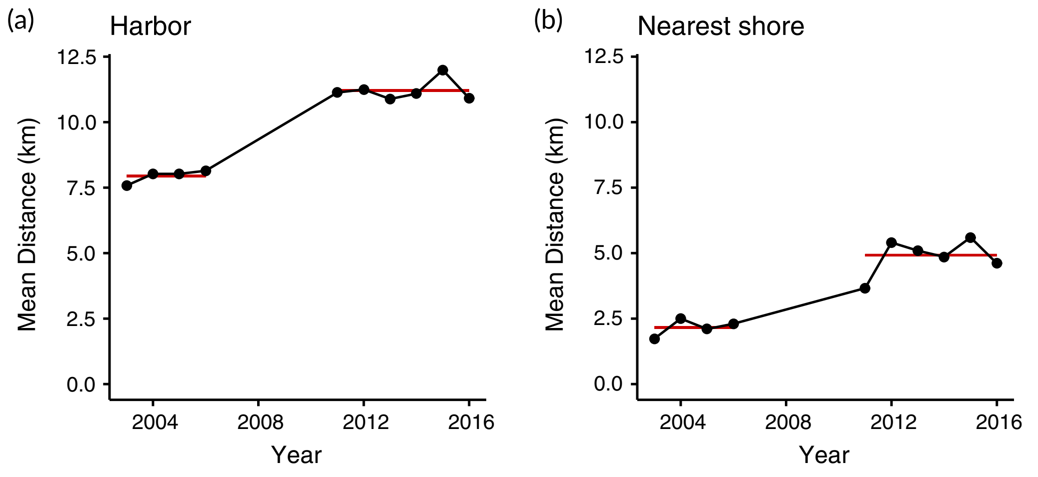


FIGURE 3 The mean distance of pilot whale encounters to Pleasant Bay harbor (a) and the nearest shore (b). Red lines indicate period means divided by changepoint analysis (Figure S1). Note 2008 is unavailable due to incomplete vessel tracks required to account for spatiotemporal autocorrelation and search effort (Table S1).

FIGURE 4 Bar plot displaying the proportion of foraging (F), resting (R), socializing (S), and traveling (T) as the predominant behaviors of long-finned pilot whale encounters in the first period (2003–2006, 2008, *n* = 1,279) and second period (2011–2016, *n* = 883) around Pleasant Bay, Nova Scotia.

to 23.0% ± 10.1%, socializing increased from 6.0% ± 2.5% to 9.9% ± 4.9% and resting increased from 11.8% ± 8.6% to 14.3% ± 8.8% (Figure 4). Traveling remained similar between the first (51.5% ± 15.5%) and second (52.8% ± 12.6%) periods (Figure 4).

Foraging hot spots were detected within the northern (i.e., Pollett's Cove) and southern (i.e., Fishing Cove) extent of the study area in both the first and second periods (Figure 5) and were consistent through time (Figure 6). Note areas of a cluster may be larger than it appears in the hot spot analysis since spatial cluster cells need neighboring cells of high occurrence (Anselin, 2018). Foraging hot spots at Pollett's Cove and Fishing Cove persisted irrespective of the shifts in encounter rate and nearshore abundance in the Pleasant Bay area. If the cells assigned as

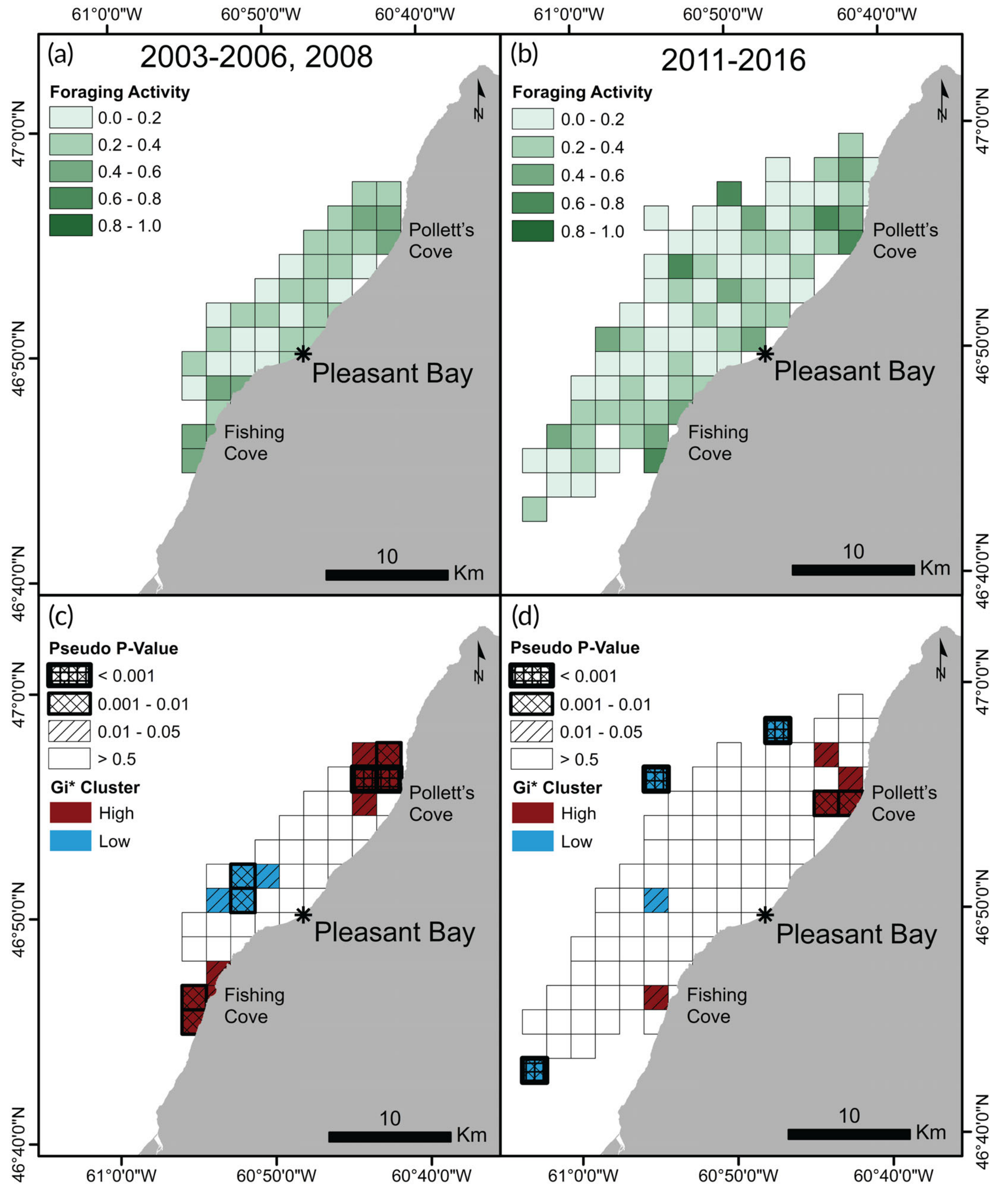
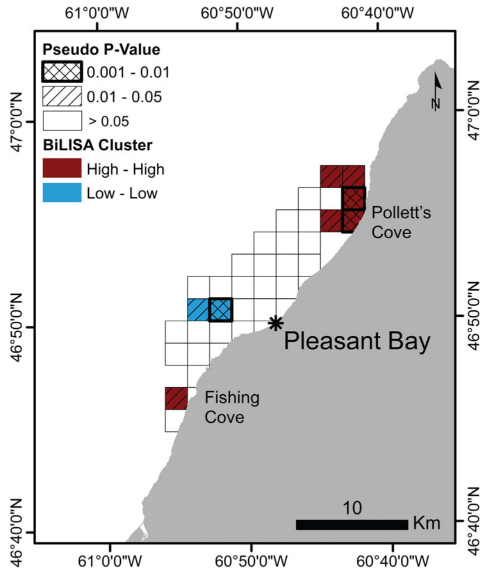


FIGURE 5 Comparison between the distribution of foraging hots pots in the first (2003–2006, 2008) and second (2011–2016) periods. Shown are the proportion of the encounters with foraging as the predominant behavior (a, b) and the associated Getis-Ord G_i* hot spot clusters (c, d). Cell size is 4 km^2 and contains ≥3 encounters.

consistent foraging hot spots (pseudo $p < .05$) are removed, eliminating 168 encounters, the overall encounter rate decreases from 1.33 to 1.24 encounters/trip. We also found a persistent absence of traveling offshore of Pollett's Cove, but no persistent socializing or resting areas within the region (Figures S1–S4).

FIGURE 6 The space–time autocorrelation of foraging activity (identified by bivariate Moran's I cluster analysis) between the first (2003–2006, 2008) and second (2011–2016) periods highlighting bivariate local indicators of spatial association (BiLISA) clusters. Cell size is 4 km^2 and contains ≥3 encounters. Note that the grid extent is smaller compared to Figure 5 as only cells with information in both periods could be included.



4 | DISCUSSION

4.1 | Space-use and behavior

Using data collected opportunistically aboard whale-watching vessels, we showed a recent shift in the distribution in the long-finned pilot whales off Pleasant Bay, Canada. In addition, we found hot spots for foraging activity around Pollett's Cove and Fishing Cove, locations that have not changed despite a decline in nearshore encounters and foraging activity. These findings confirm that long-finned pilot whales have moved farther from the shore and the long-standing view of whale-watching operators that these two coves are key foraging areas.

We documented variable yearly encounter rates around Pleasant Bay. The overall encounter rates in later years were 31% lower than in earlier years. In later years, the encounter rates were reduced nearshore and search effort extended over an area twice the size (540 km^2) of that in earlier years (272 km^2). Various factors could have driven this shift in encounter distribution between periods. For example, this shift could respond to changing prey availability, which would be supported by the observed decrease in foraging activity between periods. Water temperature in the Gulf of St. Lawrence has been increasing (Galbraith et al., 2015); and, likely due to their preference for prey sensitive to temperature increases (e.g., short-finned squid, *Illex illecebrosus*), the distribution of pilot whales in other areas has been linked to sea surface temperature (Gowans & Whitehead, 1995; Mercer, 1975). While pilot whales predominantly eat squid, their diet can also include other small invertebrate or fish species (Mercer, 1975; Nøttestad et al., 2015). Shifts in ecosystem structure due to fisheries in the Gulf of St. Lawrence (Morissette et al., 2006; Savenkoff et al., 2007, 2013) could result in pilot whales changing their preference to more offshore prey, and thus could also explain the observed changes in distribution. However, we showed that the foraging hot spots nearshore were stable over time, suggesting some consistency in the nearshore occurrence of prey.

Increased whale-watching activity may also have contributed to the change in pilot whale distribution. While encounter distance increased 2.71 km from the nearest point on the shore across periods, the distance from the harbor increased by 3.27 km. The more considerable change concerning the harbor, where there is the highest whale-watching boat density, may suggest avoidance to vessels. However, a similar scale in the changes between harbor and shoreline hinders our capacity to assess whether whales avoid whale-watching vessels or are moving away from shore due to prey availability or other environmental changes. Challenges in differentiating between whale-watching pressures and impacts on cetaceans from other extrinsic or intrinsic factors are commonly recognized (IWC, 2019). While the effects of whale-watching are generally challenging to ascertain (Johnston, 2014), shifts in the distribution of whales beyond the range of whale-watching operations can indicate whale-watching activity is affecting whale movement (Bejder et al., 2006; Lusseau, 2005; Tyne et al., 2014). While the Canadian guidelines permit whale-watching vessels to approach most whale species to 100 m (DFO, 2018), vessels within 183 m have been shown to disrupt the feeding behavior of other cetaceans (Lusseau et al., 2009). When the energetic cost incurred from tolerating vessel disturbance is higher than the energetic gain, animals may relocate to more favorable locations (Christiansen et al., 2013; Senigaglia et al., 2016). While our results suggest lower encounter rates during 2016, the recovery of encounter rates in more recent years (E. Zwamborn, personal communication, May 6, 2019) suggests that current levels of whale-watching pressure may be within the tolerance limits of pilot whales. While our study did not ascertain the mechanism for the observed shift in distribution, we demonstrate that data collected aboard opportunistic platforms can monitor distributional shifts in whale populations and set the stage for further research investigating the factors associated with shifts in distribution.

Regardless of the mechanisms driving the changes in encounter rates, due to the paucity of nearshore sightings in the second period of our study, whale-watching operators had to increase the duration of their trips to accommodate the increased search effort and travel distances. In turn, this reduced the number of excursions from five to three trips per day and the number of ticket sales they could make a day.

4.2 | Implications for management

Optimizing the trade-off between ecological sustainability and economic viability of whale-watching tourism in an area necessitates ecological information on the target species. Our results can provide useful information for a precautionary approach to the management of the target species.

As anthropogenic disturbance in energetically important areas can decrease whale occurrence in the area (Bejder et al., 2006), limiting vessel disturbance in these foraging areas could have a disproportionately positive effect on the whale population (Williams et al., 2006). The hot spots off Pollett's Cove and Fishing Cove are relatively small spatial areas, with a combined area of 20 km^2. Limiting whale-watching within these areas would lower the whale-watching sighting rate from 1.33 to 1.24 encounters/trip, a decline much smaller than the one observed across periods (1.57 to 1.09 encounters/trip). Whale-watching outside foraging hot spots would have limited immediate impact on access to pilot whales while reducing the potential effects of anthropogenic disturbance. Other mitigation measures, such as developing a voluntary code of conduct suggesting greater distances between vessels and whales in these areas, could be employed to reduce potential impacts (Allen et al., 2007; Guerra & Dawson, 2016).

While we focus on foraging hot spots, it is crucial to assess whether other behaviors can be affected by anthropogenic disturbance before identifying areas where to limit whale-watching. Foraging in pilot whales can be disrupted by anthropogenic activity (Isojunno et al., 2017), and generally, whale-watching is known to affect foraging (Christiansen et al., 2013; Meissner et al., 2015; Stockin et al., 2008). However, other behaviors such as resting can also be affected by human activity and have repercussions on the population in other cetaceans (Lusseau & Higham, 2004; Stockin et al., 2008, Tyne et al., 2015). Limiting whale-watching activities close to foraging whales could inadvertently increase disruptions to other sensitive behaviors, such as resting (Agardy et al., 2011). Here, there was no evidence for consistent resting hot spots across years (Figures S2 and S5), and compared to the foraging activity that decreased, the amount of resting behavior slightly increased across periods (Figure 4). As such, in our study, the focus is on foraging behavior for area-based management. Regardless, ensuring whale-watching operations do not disrupt other sensitive behaviors as a result of shifting away from foraging hot spots is essential (Agardy et al., 2011). Further mitigation measures, for instance, increasing the distance between vessels and whales when displaying sensitive behaviors such as resting, may help limit anthropogenic disturbance.

There is a growing effort to recognize and protect areas vital to cetaceans to reduce anthropogenic disturbance (Ashe et al., 2010; Filby et al., 2017; Gormley et al., 2012). Although the two key foraging areas identified were persistent during this study, implementing small-scale management in the form of a fixed restricted zone may not suffice (e.g., Hyrenbach et al., 2000). While Marine Protected Areas (MPAs) can offer protection and may draw more tourism to the region (Eagles et al., 2002), they are slow to implement and often face heavy pushback in areas similar to Pleasant Bay, where fishing is an essential livelihood (Bennett & Dearden, 2014). In addition, cetacean species have dynamic space-use patterns and fixed restricted zones can quickly become irrelevant to the species of interest (Filby et al., 2017; Hartel et al., 2015; Hyrenbach et al., 2000; Wilson et al., 2004). For instance, common bottlenose dolphins (*Tursiops truncatus*) in New Zealand have shown enough plasticity in space use to render their initial MPA ineffective after 5 years (Hartel et al., 2015). Flexible management strategies focusing on integrative and adaptive frameworks encompassing activity and habitat-based knowledge have been proposed as the most effective means of protection (Higham et al., 2008, 2016; Tyne et al., 2014). This management could take the form of an informal agreement between local marine wildlife tourism companies. Continued collaborative monitoring is key to the success of adaptive management systems; thus, the potential for continuous cost-efficient data collection makes whale-watching vessels a great platform to gather data for local management (Currie et al., 2018; Hupman et al., 2015). Valuing local knowledge is at the root of a collaborative management system. This integrated monitoring system has additional benefits of building relationships between scientists and industry operators as well as providing a platform for public education.

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AUTHOR CONTRIBUTIONS

Sarah McComb-Turbitt: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; validation; visualization; writing-original draft; writing-review & editing. **Joana Costa:** Conceptualization; data curation; writing-review & editing. **Hal Whitehead:** Conceptualization; data curation; funding acquisition; methodology; project administration; resources; supervision; writing-review & editing. **Marie Auger-Méthé:** Conceptualization; data curation; methodology; project administration; resources; software; supervision; validation; writing-review & editing.

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Additional supporting information may be found online in the Supporting Information section at the end of this article.

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